

POPULATION BIOLOGY OF *TRISOPTERUS MINUTUS CAPELANUS* (GADIDAE) FROM THE EASTERN COAST OF GREECE

by

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ABSTRACT. - A total of 35650 *Trisopterus minutus capelanus*, poor cod, collected by trawling off the eastern coast of Greece (Euvoikos Gulf, Pagassitikos Gulf and Orei Channel) between September 1986 and June 1988, were analysed. Otoliths from 457 specimens were used for age and growth studies together with length-frequency data. From the validation techniques the analysis of marginal increments was selected. A single annulus forms each year on the otolith. Back-calculation of size at age showed that males were generally smaller than females, especially for fish more than one year old. The growth of poor cod was described by a von Bertalanffy growth curve with parameters $K = 0.18$, $K = 0.32$ and $t_0 = -1.83$, $t_0 = -1.62$ for females and males respectively. The length-weight relationship was obtained for the total of individuals and $b = 3.2$ was used to estimate the condition factor. The condition factor has a maximal value in winter and decreases significantly during summer. The overall sex ratio shows a prevalence of females. Males begin to mature at a size of between 10-11 cm and females between 11-12 cm. The spawning period extends from winter to summer with a peak during spring. The computed value of natural mortality was 0.44 and the mean total mortality rate for the two years studied was 0.87.

RÉSUMÉ. - Un échantillon de 35650 *Trisopterus minutus capelanus*, récolté sur la côte est de la Grèce (golfe d'Euvoikos, golfe de Pagassitikos et canal d'Orei) entre septembre 1986 et juin 1988, a été analysé. Les otolithes de 457 spécimens ont été utilisés pour étudier l'âge et la croissance, en association avec les données des fréquences de taille corporelle. L'analyse de l'accroissement marginal des otolithes a été retenue à la suite de tests de validité. Un seul annulus se forme chaque année sur l'otolithe. Le rétro-calcul de la taille à âge connu montre que les mâles sont généralement plus petits que les femelles, et ceci plus particulièrement pour les poissons de plus d'un an. La croissance de *T. m. capelanus* suit une courbe de von Bertalanffy avec comme paramètres $k = 0.18$, $k = 0.32$ et $t_0 = -1.83$, $t_0 = -1.62$ pour les mâles et les femelles respectivement. La relation longueur-poids est calculée pour l'ensemble des individus et $b = 3.2$ a été utilisé pour estimer le facteur de condition. Ce dernier atteint une valeur maximale en hiver et décroît significativement pendant l'été. Le sex ratio est en faveur des femelles. La maturation des mâles commence à une taille comprise entre 10 et 11 cm et celle des femelles entre 11 et 12 cm. La période de ponte s'étend de l'hiver à l'été avec un pic pendant le printemps. La valeur calculée pour la mortalité naturelle est de 0,44 et le taux moyen de mortalité obtenu sur les deux années d'étude est de 0,87.

Key-words. - Gadidae, *Trisopterus minutus capelanus*, MED, Greece, Age determination, Otoliths, Growth.

Two subspecies of the species *Trisopterus minutus* exist in the European sea waters, *T. m. minutus* and *T. m. capelanus*. They are usually separated on the basis of geographical range, overall size, meristic and morphological characters. *T. m. minutus* ranges from Trondheim Fjord to Gibraltar, whereas *T. m. capelanus* is found off Morocco and in the Mediterranean Sea (Whitehead *et al.*, 1986). The biology of *T. m. minutus* in the Atlantic Ocean has been studied by different

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authors (Menon, 1950; Labarta, 1976; Cooper, 1983) but there have been few investigations on the biology of *T. m. capellanus* in the Mediterranean Sea. Planas and Vives (1952) and Vives and Suau (1956) described various aspects of *T. m. capellanus* life history from the Spain coasts. Because of its relative importance as a commercial species some data about its biology have been presented in the General Fisheries Council for the Mediterranean (FAO) meetings the last years (1980, 1981). Tangerini and Arneri (1980) and Frogia (1981) provided some information on growth, distribution and spawning of *T. m. capellanus* of the Adriatic Sea, and recently, Gianetti and Gramitto (1988) have estimated its age and growth by using otoliths. Published information on the life history of *T. m. capellanus* in the seas around Greece is limited to notes on geographical distribution (Ondrias, 1971; Economidis, 1973; Papaconstantinou, 1988), its fishing status (Papaconstantinou *et al.*, 1989) and feeding ecology (Politou *et al.*, 1989a; Politou *et al.*, 1989b).

In view of the development of commercial fisheries for *T. m. capellanus* in the Greek seas we have prepared this account to estimate the biological characteristics of its stock, such as growth rates, length distributions, reproduction as well as mortalities and yield per recruit.

MATERIAL AND METHODS

The Pagassitikos Gulf, Euvoikos Gulf and Orei Channel form semi-enclosed inlets of sea situated along the central eastern coast of Greece (Fig. 1). Only in the N.E. part of the Euvoikos Gulf the depth does exceed 400 m. The sea bed in these areas consists of soft mud, sandy mud and *Possidonia* beds in the shallow water. Trawl fishing has been prohibited in the Pagassitikos Gulf, the Orei Channel and the northern part of the Euvoikos Gulf since 1960. In the remaining part of the Euvoikos Gulf the trawl fishing is permitted from the beginning of November to the end of March. From September 1986 to June 1988, seasonal



Fig. 1. - Map of sampling areas showing the fishing stations.

sampling surveys were carried out at 24 stations using a 500 HP motorboat towing a net with a cod-end mesh of 28 mm between stretched knots. Trawl hauls were standardized as far as possible to last 20-30 min depending on weather conditions, nature of the sea bed and depth.

During the surveys a total of 35650 *T. m. capelanus* were collected. Fish total length (TL) and weight were taken to the nearest millimeter and gram respectively. Both otoliths (sagittae) were removed and preserved in labelled vials containing a 50:50 glycerin water solution. Before reading they were placed in cold mounting resin and cut longitudinally through the nucleus with an electric low-speed saw, to prepare sections about 0.5 mm thick. The cut was performed by two rotary saws 0.5 mm apart. The otolith sections were placed on a black background and the opaque zones were examined in reflected light. After counting the number of rings, the distance was measured from the focus to the distal edge of each annulus and to the otolith edge along the sulcus acousticus, most closely perpendicular to the otolith edge (Fig. 2).

From the validation techniques described by Bagenal and Tesch (1978) the analysis of marginal increments was used. The measurements of the otoliths were made from the focus to the posterior margin (R) and to the last annual growth mark ($R_{n_{i,\dots,n}}$). The difference between these two measurements represented the marginal otolith increment ($R - R_{n_{i,\dots,n}}$) since the last annulus was formed. This marginal otolith increment should be maximal just before, and minimal just after, the formation of the last annulus. As the growing season progressed, the location of the last annulus became more distant from the edge of the otolith. Only the most abundant age groups available throughout the year groups (I to III) were used. Growth was modelled with the von Bertalanffy growth curve fitted to back-calculated lengths for ages 1-5. Von Bertalanffy parameters, asymptotic length L_∞ , growth coefficient k and time of zero length t_∞ were determined using the method of Tomlinson and Abramson (1971).

Total mortality was calculated by the catch curve method as modified by Pauly (1983). The natural mortality (M) was computed by the relationships:

$$\log M = -0.0066 - 0.279 \log L_\infty + 0.6534 \log k + 0.4634 \log T, \text{ (Pauly, 1980) and}$$

$$\log M = \log 3 + \log L_\infty + \log k + \log(1 - L_T / L_\infty) - \log L_T, \text{ (Roff, 1984),}$$

where k is the growth coefficient, L_∞ the asymptotic length in cm, T is the mean annual temperature of the sea water and L_T the length at the first maturity.

The yield per recruit was calculated using the analytical model of Beverton and Holt (1957) as simplified by Gulland (1983).

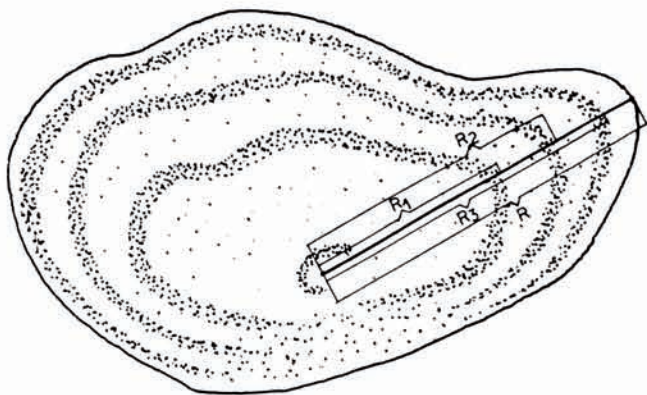


Fig. 2. - Otolith section of a *T. m. capelanus* of age group III: R = otolith radius, R1, R2 and R3 = distances from the centre of the first, second and third annulus respectively.

RESULTS

Length frequency distribution

The length frequency distributions of *T. m. capelanus* are presented in figure 3. Its total length examined in different seasons and locations ranged from 50-310 mm, however fish longer than 280 mm were scarce. *T. m. capelanus* were found in depths of 25-310 m, but it was most abundant in depths of 50-100 m in all regions studied. Due to an extended spawning season, insufficient information about the migration behaviour, and the lack of constant fishing effort between the different areas studied, the seasonal length frequency histograms are difficult to interpret. Age I fish were estimated to be about 12-13.0 cm in March 12-15.0 cm in June, 14-16.0 cm in September and 15-17.0 cm in December. Age II fish were approximately 15-17.0 cm in March-June, 16-18.0 cm in September and 17-18.0 cm in December.

Figure 3 illustrates the seasonal length increments exhibited by the 1986 year class throughout the study period. The seasonal progression of these modal groups offers an excellent opportunity to study early growth and evaluate results from ageing of otoliths. Young-of-the-year were represented by a modal length which ranged between 9 and 11 cm. Thus, in the Euvoikos Gulf they first appeared in the survey catch in autumn (5-12 cm), whilst in the Pagassitikos Gulf and Orei Channel they appeared during summer (5-10 cm). The dominant age-0 fish in autumn and summer can be almost easily followed from September or June (6-9.0 cm) through next June or March respectively, where they were assigned to age group I (12-13.0 cm). The data presented in the above figures show that the 1986 year class reached 40% of the catch from Euvoikos Gulf and the 1987 year class represented up to 85% and 72% of the catches from Pagassitikos Gulf and Orei Channel respectively. The abrupt decrease in the abundance of the larger than 14.0 cm individuals in the Euvoikos Gulf during December, which is not found in the other areas, coincides with the beginning of the trawl fishery (1st November) giving strong evidence of differential mortality among the areas. On the other hand other biological or ecological factors such as migration or dispersion might result in a decrease in the abundance of *T. m. capelanus* in the samples during spring or summer, which is observed in all the areas.

Marginal increment analysis

The alternating pattern of hyaline and opaque zones on *T. m. capelanus* otolith's sectioned surface was easily distinguishable, particularly the first two-three annuli which were readily observed to be continuous around the otolith. For annuli formed later, particularly those beyond the third, this pattern was less distinguishable and the hyaline zone could not be traced around the whole otolith.

Marginal increment analysis indicates that a single annulus forms each year (Fig. 4). Some age I individuals seem to have already formed their annual mark in March, whilst most of them show maximal marginal distance during this month. In age II and older individuals the annulus formation seems to take place earlier, between December and March.

This could be attributed to the fact that some specimens may have formed their first discernible otolith annulus when they were older than 12 months, because the species spawns all through the year, with a peak during spring. With this protracted spawning season it is reasonable that in many fish the first annulus mark would not be formed after exactly 1 year. Fish that hatched early may have formed a mark within a few months of hatching, but in this case it would be close to the focus and probably too indistinct to be counted as an annual mark. Under these conditions the next mark would have been formed after an interval of more than 12 months after hatching. In contrast, fish that hatched late could have formed the first strong mark after less than 1 year.

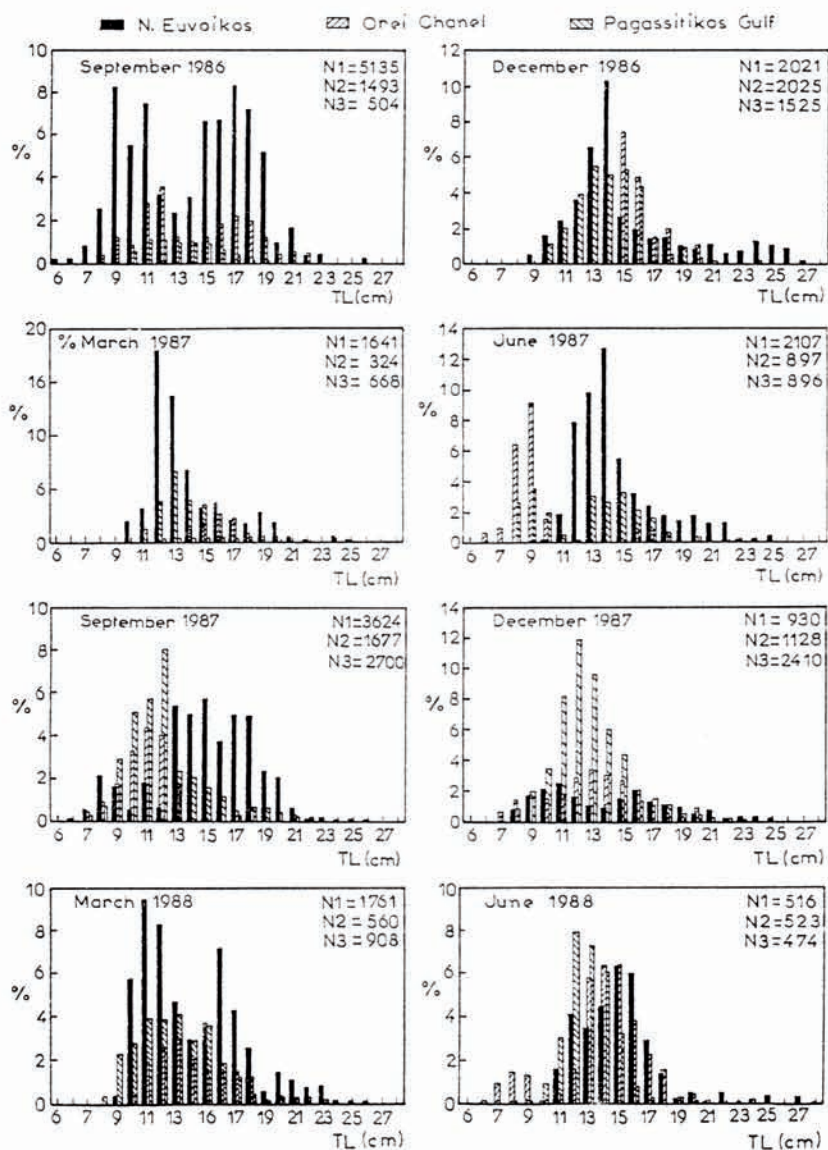


Fig. 3. - Seasonal length-frequency distribution of *T. m. capelanus* captured by trawl off the eastern coast of Greece from September 1986 to June 1988. (N1 = number of specimens measured from Euvoikos Gulf, N2 = number of specimens from Orei Channel, N3 = number of specimens from Pagassitikos Gulf).

All marks after the first one would have been at annual intervals. The balance between these two cases determines the average growth before the first counted mark. The average growth period for age I fish in this study seems to be more than 12 months.

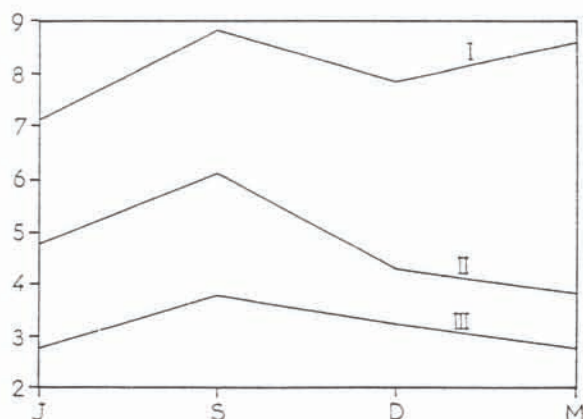


Fig. 4. - Marginal otolith increment of *T. m. capelanus* for age groups I, II and III. (J = January, S = September, D = December, M = March).

Growth

Length in terms of age were back-calculated from the otolith radius / fish length regression derived by plotting the radius of the otolith section on total fish length. The linear relationship was used to back-calculate total length at earlier ages using the methods adopted by Bagenal and Tesch (1978), Ricker (1975), Everhart *et al.* (1975). Coefficient of correlation, regression coefficient and standard error estimates indicated that the linear relationship fits well the data. Growth appears to be slightly better in the Euvoikos Gulf; however there is no consistent difference (t test $P < 0.05$) from Pagassitikos Gulf and Orei Channel.

An analysis of covariance test showed a significant difference between sexes ($F = 5.3$; $df = 1$, $P < 0.05$), thus the relationship between the otolith radius (R) and total length (TL) is given separately for each sex:

$TL = 16.959 + 2.889 R$, ($r^2 = 0.73$) for males

$TL = 16.103 + 3.042 R$, ($r^2 = 0.79$) for females.

Back-calculated size at age of males was generally smaller than that of females (Table I). The growth doesn't differ statistically (t test, $P < 0.5$) between sexes for age I individuals. However the difference becomes larger for older specimens and is not significant for age II ($P < 0.2$) and for age III individuals ($P < 0.1$). This difference could be associated with the earlier age of maturity (10-11.0 cm) of males, compared with females (11-12.0 cm). The longevity of females also generally exceeded that of males, thus those of age V were represented by females only as no males were caught. The low representation of males in the older age groups give strong evidence for differential mortality among the sexes.

The relation between otolith radius and total length for both sexes combined is given by the equation:

$TL = 11.78 + 3.07 R$, ($r^2 = 0.83$)

whereas the back-calculated length at each age are given in the table I. Back-calculated length did not display Lee's phenomenon at all five annuli.

Von Bertalanffy growth curve

The von Bertalanffy growth model applied for *T. m. capelanus* was expressed by the following equations:

Females $L_t = 334.5[1 - e^{-0.178(t+1.825)}]$

Males $L_t = 232.7[1 - e^{-0.315(t+1.624)}]$

Combined sexes $L_t = 322.7[1 - e^{-0.179(t+1.867)}]$

where maximum-length is given in mm.

Table I. - Comparison of back-calculated length of male and female *T. m. capellanus* and back-calculated mean length for the entire population.

Age	N	Mean length at capture (mm)	Mean back-calculated length (mm)				
			I	II	III	IV	V
Males							
I	37	155	131				
II	10	174	124	158			
III	5	199	129	159	174		
IV	1	223	144	167	182	193	
V	-	-	-	-	-	-	-
N			55	16	6	1	-
Mean length/age			130	159	175	193	-
Standard deviation			12.3	14.6	13.7	-	-
Annual increment			130	29	16	18	-
Females							
I	61	153	130				
II	25	180	136	167			
III	14	210	128	165	189		
IV	9	223	128	167	190	205	
V	2	249	133	182	212	226	235
N			111	50	25	11	2
Mean length/age			131	167	191	209	235
Standard deviation			11.1	11.5	13.3	12.8	3.0
Annual increment			131	36	24	17	26
Comparison of variances (P=0.05)			F=1.6 F<Fv1, v4		F=1.1 F<Fv1, v4		- -
Comparison of mean length			Z=0.53 Z<1.96 P=0.05	t=2.23 t>t0.05/0.05 t<t0.05/0.05	t=2.54 t>t0.05/0.05 t<t0.05/0.05		
Males + Females							
N			362	142	56	19	4
Mean length/age			129	163	186	205	228
Annual increment			129	34	23	19	23

Length-weight relationship

During the course of the survey a total of 4519 specimens were weighed and the length-weight relationship was computed:

$$W = 0.005863 \times L^{3.21} \quad r^2 = 0.96 \quad (\text{St.er.} = 0.0098)$$

where W = weight in grams, TL = total length in cm and r^2 = regression coefficient. The slope was greater than 3, indicating that *T. m. capellanus* become progressively "plumper" with increase in length.

The condition factor was measured using the equation: $K = \frac{100 \times W}{TL^b}$

where W = total weight in g, TL = total length in cm and b = 3.217, the constant calculated from the length-weight relationship.

The seasonal variation of K (Fig. 5) shows a peak during winter for both years studied; in spring it decreases significantly, whereas in summer there is a further decrease or it remains at the same level. Condition tends to increase again in autumn.

Reproduction

Almost 2500 *T. m. capellanus* (1011 males and 1502 females), collected in 1986-88 were examined to determine the period of the reproductive activity. Specimens with spent and ripe gonads were found in the whole area during almost all seasons, however maximum spawning activity was observed in spring. The spawning period of *T. m. capellanus* in the Euvoikos Gulf begins a little later than in the other areas, as could be suggested by the lower percentage of mature fish in March (Fig. 6).

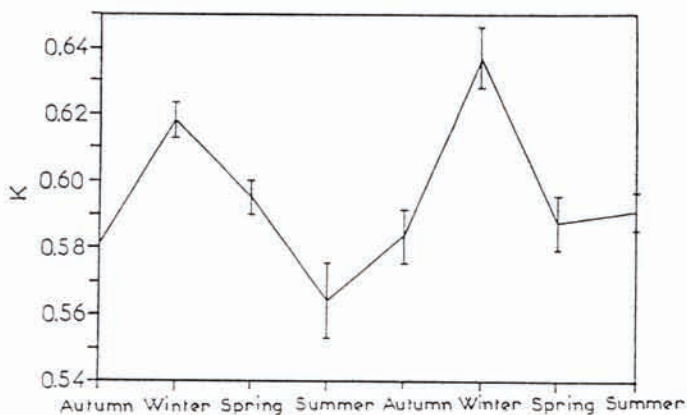


Fig. 5. - Seasonal variation of condition factor (K) of *T. m. capellanus* from autumn 1986 to summer 1988 with confidence limits of 95% marked.

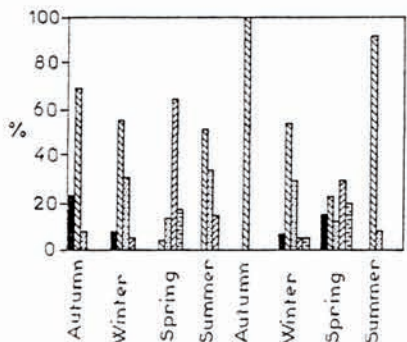
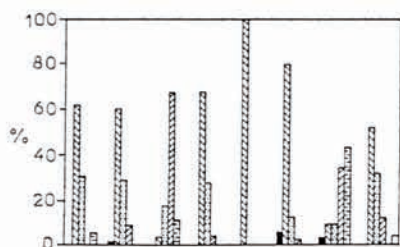
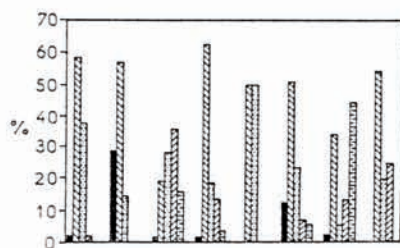


Fig. 6. - Percentages of different maturity stages per season for female *T. m. capellanus* in the areas of a) Euvoikos Gulf, b) Orei Channel and c) Pagassitikos Gulf.

■ Stage I ▨ Stage II □ Stage III
 ▩ Stage IV ▤ Stage V □ Stage VI

Males begin to mature at a smaller size (10-11.0 cm) than females (11-12.0 cm). Medium size at first maturity is taken during the peak of the reproductive activity and the length at which 50% of the specimens are mature is 14 cm, which corresponds to the end of the first year of life.

Sex ratio

Based on the seasonal samples of the year, the general sex ratio for *T. m. capelanus* (♂:♀) was found to be 0.60 for both years of the study. A chi-square test indicated significant difference ($P < 0.05$) from the expected 1:1 ratio (1986-87: $\chi^2 = 7.7$; 1987-88: $\chi^2 = 6.9$). The sex ratio of the species varies considerably as a result of differential behaviour and mortality rates between the sexes. On the other hand the predominance of females with increasing age causes a general tendency for the sex ratio to favour females.

Mortality

Since *T. m. capelanus* were not fully recruited to the trawl fishery until age I, total mortality (Z) estimates from catch-curves were based on fish age I and older. The von Bertalanffy growth curve derived from the survey data was used to convert the length frequency data to age frequency (Pauly, 1983). The slope of the descending limb corresponds to the total mortality rate Z.

The calculated values of Z are shown in table II for the total catch for the fished, unfished and combined areas. It is worth noting that the total mortality rate of *T. m. capelanus* in the unfished areas is higher than in the fished areas. This is unrealistic because the Z of an unfished population is always lower than the Z of a fished one where both fishing (F) and natural (M) mortality occur. However, this phenomenon can be explained by the different size distribution of the species in the two areas, taking into account that there is a dominance of small specimens in the unfished area. For these reasons the calculation of M is based on the relationships proposed by Pauly (1980) and Roff (1984). If the L_{∞} , K and L_{50} values from the previous sections are inserted in these equations, M is calculated 0.44 and 0.63 respectively. Taken in consideration that in the gadoid species the value of M is 2 to 3 times the value of K (Gulland, 1983) the M calculated using Pauly's method must be retained.

Area	1st year	2nd year
Total	0.84	0.90
Fished	0.73	0.75
Unfished	0.86	1.07

Table II. - Total mortality rate (Z) values of *T. m. capelanus* using PAULY's method (1980).

Yield-per-recruit (Y/R)

Our estimates of growth and mortality parameters provide all the information necessary to compute the yield-per-recruit of *T. m. capelanus* as function of age at first capture (T_c) and fishing mortality rate (F). In the study area, at least now, young *T. m. capelanus* are vulnerable to capture at $T_c = 0.5$. The yield per recruit relation to F is shown in Figures 7 and 8 for different values of T_c and M respectively. The maximum Y/R at $T_c = 0.5$ is 16.3 g for a fishing mortality rate of 0.65 (Fig. 7). The product of the Y/R at the target fishing mortality of $F = 0.42$ is 16.0 g. The plots show that an increase in the commercial harvest under present regulations would result in over-exploitation, particularly if the natural mortality rate is lower than that estimated. Any increase in fishing effort must be accompanied by an increase in the age of first capture ($T_c > 1$) in order to get a better Y/R and avoid over-exploitation.

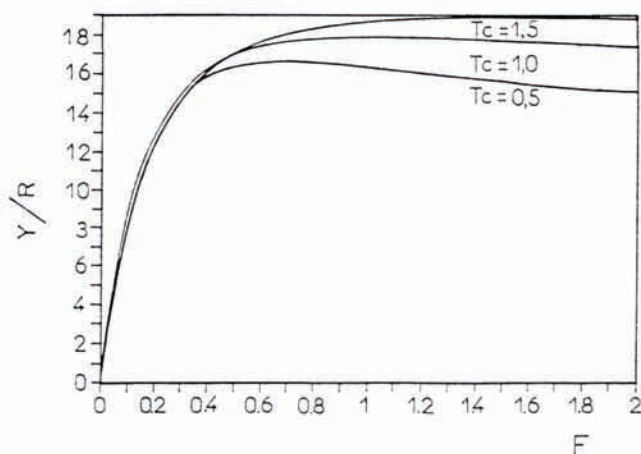


Fig. 7. - Relation between Y/R and fishing mortality rate (F) of *T. m. capelanus* for different age of first capture (T_c).

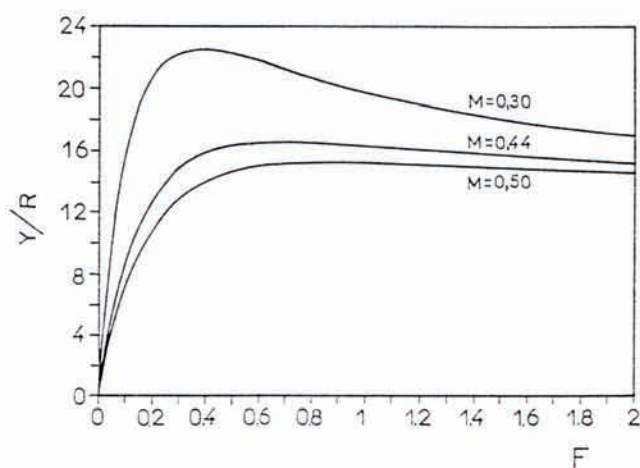


Fig. 8. - Relation between Y/R and fishing mortality rate (F) of *T. m. capelanus* for different values of natural mortality rate (M).

DISCUSSION

The analysis of the survey data indicates that pre-recruit and commercial-size *T. m. capelanus* occupy the same areas. Vives and Suau (1956) reported that both immature and mature *T. m. capelanus* along the mediterranean Spain coasts are found together, throughout a wide depth zone. The differences in the age composition of the stocks at the different stations/areas was almost certainly related to depth. Papaconstantinou *et al.*, (1989) have shown the initial presence of the 0-group fish in the depth zone 50-100m in the N.Euvoikos Gulf, Orei Channel and

Pagassitikos Gulf, and in addition they were also abundant in depths >100 m in the first area.

The back-calculation technique has normally been applied to otolith measurements, but the first growth ring is usually not well-defined in *T. m. capelanus*. Thus the validation of the ageing technique was indispensable. Although a mark-recapture study is the only true means of validation (Beamish and MacFarlane, 1983) other alternative methods are also used for this purpose. The marginal increment analysis method indicated that a single annulus was formed each year in the otoliths of *T. m. capelanus*. Back-calculation of fish length agreed reasonably with length at capture of corresponding age groups. Differences, such as the larger mean observed than back-calculated length, are attributed to growth following mark formation. Growth which was relatively fast for the first year, drops sharply in the second year and decline slowly thereafter (Table I). Annual growth increment were only 3.4 cm for age group II, 2.3 cm for age group III and 1.9 cm for age group IV. The mean increment value calculated for age V is of doubtful accuracy because of the small sample size and because annuli of these older fish are extremely close together and therefore difficult to measure precisely.

Few growth studies of *T. m. capelanus* have been published. Our back-calculated total lengths for age 1-5 compared favourably with total length for the same age calculated by Tangerini and Arneri (1984) in the Adriatic Sea. Growth presented by Planas and Vives (1952) was slightly less than that presently calculated. The differences may be the result of geographical variation in growth rates, gear selectivity, levels of exploitation, or other ecological factors.

The growth coefficient (0.18) indicates slow attainment of maximum size for the females and combined sexes, faster for the males ($k = 0.32$) and both were lower to that of the E. Mediterranean, $K = 0.59$ (GFCM-FAO, 1981, 1982) and Adriatic Sea $K = 0.48 - 0.84$ (Gianetti and Gramitto, 1988). In general the growth of *T. m. capelanus* in the Greek seas seems to be different to that of other parts of Mediterranean, apart from the Adriatic Sea, where the males attained the same maximum length.

The low representation of males in the older age groups, associated with the longevity of females give strong evidence of differential mortality among the sexes. The variation in growth pattern between sexes was the result of a higher decline in growth rate of male fish after the first year of life in comparison to the females. The most likely factor responsible for the decline in growth rate was sexual maturation of the fish, which often causes a discontinuity in the growth (Beverton & Holt, 1957). The actual mechanism behind these distinct growth patterns is uncertain but, because of the close association with sexual maturity, it is probably a strategy for maximizing the reproductive capacity of the species. *T. m. capelanus* accomplished almost the one-half of their linear growth during the first year of life.

The reproductive strategy of *T. m. capelanus* tends to maximize reproductive potential and avoid catastrophe. The strategy is a combination of extended spawning season with variable duration, early maturation (end of the first year), high fecundity, serial spawning and extensive migration across the continental shelf during spawning. The five to seven month spawning season reduces larval competition and decreases the impact of predators and adverse environmental conditions on the survival of eggs and larvae. Results obtained here for individually and group-reared males illustrate the importance of sexual maturity in studies of growth rate and body size of fish. Variances in length and weight, including the partitioning of the variance into observed and casual components, may be markedly affected by sexual maturity. For example, in salmonid fishes, early sexual maturity is recognised as a major cause of small adult size (Iwamoto *et al.*, 1984) while fast growth rate is believed to be a cause of early sexual maturity (Saunders *et al.*, 1982).

Other studies have also shown that *T. m. capelanus* spawns for a long period of the year. Planas and Vives (1952) and Vives and Suau (1956) reported

that along the east coast of Spain the species spawn from January to May, whilst Frogliia (1981) and Tangerini and Arneri (1984) mentioned that in the Adriatic Sea it spawns between January and May or June. In the last two papers it is also stated that the poor cod matured at about 13.0 cm TL, which is close to the length found in the present study (14 cm).

If M is 0.44 per year, then the Z estimation for the unfished areas with the catch curve method seems to be high; however, as there is an abundance of small fish in the different depths with a preponderance of larger fish in deeper waters, the high mortality rate of the species in the unfished shallower areas is likely to be a reflection of the length frequency distribution, and of the migration of larger and hence older fish, into deep water out of the unfished area.

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